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POSTURE AND MOVEMENT: COORDINATION AND CONTROL

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INTRODUCTION

Body posture depends on a highly integrated, multisensory system of control (51, 55, 66). This system includes several feedback loops that use visual, vestibular, and somatosensory information. Classical studies emphasized the role of chain of reflexes starting from different peripheral sensors as the basic building blocks of postural mechanisms, such as the stretch reflex (68), head and neck reflexes (47) and righting reflexes (64). Giuseppe Moruzzi, his colleagues and students contributed to reveal the crucial role played by several central neural structures in the homeostatic regulation of postural muscle tone, in particular the role of the cerebellum, brainstem reticular formation and intraspinal circuits (56). In Moruzzi's Institute Carlo Terzuolo, who should later introduce us to the field, developed his own interests in postural tone through a series of studies dealing with cerebellar inhibitory and excitatory effects on motoneurones (72, 74). In Minneapolis he subsequently applied the approach of systems analysis to quantify the behaviour of the stretch reflex in decerebrate cats (62, 67) and in man (73), and vestibulospinal reflexes in cats (2). Following these lines, we have extended the analysis of posture to normal, behaving cats (37, 39, 40, 42) and carried out related work in man (10, 33, 34, 35), also in collaboration with Carlo Terzuolo (43, 70). This work is reviewed here in the context of current views on postural mechanisms and on the control of limb movements (see also 32, 38, 41).

I. *Reflex mechanisms for postural control.*

In decerebrate cats, vestibulospinal and tonic neck reflexes tend to exert antagonistic effects on forelimb muscles, and thus may cancel in response to head tilts about a stationary trunk (19, 44, 50). It has been hypothesized that the functional significance of this reflex interaction for postural control consists in the stabilization of trunk orientation in space when the whole animal is moved (53, 65). According to this hypothesis signals from neck receptors encoding the orientation of the head relative to the trunk would be subtracted from vestibular signals encoding head orientation relative to the gravity vector, thus providing an error signal proportional to the deviation of the trunk from the vertical. However, despite its logical appeal, there a number of difficulties with this hypothesis. First, the gain of vestibular and neck reflexes is direction-dependent. Using multidirectional rotations, it has been found that the vestibular and neck response vectors of elbow extensor muscles tend to cluster around roll, whereas the gain in pitch is quite low (78). For shoulder muscles, vestibular vectors are also close to roll, but a nose-up pitch component is observed in neck responses (78). Moreover, the response vectors of vestibular and neck reflexes remain stable over the low to midfrequency range, but their gain and phase diverge at higher frequencies due to the greater velocity sensitivity of vestibular inputs over that of neck inputs (77). In sum, only partial cancellation of the two reflexes is to be expected: effective reflex interaction occurs mostly around roll and in the low- to midfrequency range.

The behaviour of these reflexes is strictly correlated with that of vestibular neurons. A high degree of convergence between vestibular (otolith and canal) and neck inputs has been found in the lateral and inferior vestibular nuclei (12, 29). Best directions of activation of neurons in these nuclei tend to cluster around roll (±45°), the direction for vestibular stimuli being roughly opposite to that for neck stimuli. Gain and phase for vestibular and neck inputs are coherent for neurons with predominant otolith inputs, and for those with otolith plus canal inputs. Responses are more divergent in the case of neurons with canal inputs only (29). Also the responses of pontomedullary reticulospinal neurons to vestibular stimuli are oriented around roll (9, 50a, 61c). It has also been shown that the locus coeruleus can modulate the gain of vestibulospinal reflexes in roll by means of either a direct coeruleospinal pathway or an indirect pathway via pontomedullary reticulospinal neurons (3, 61b). In precollicular decerebrate cats, the gain of vestibulospinal and neck reflexes can be quite low as a result of an increased discharge of noradrenergic neurons of locus coeruleus (61a).

Postural mechanisms are obviously more complex in intact, behaving animals. In particular, the contribution of vestibular and neck reflexes to postural stabilization may not be as prominent as in decerebrate cats, due to a lower reflex gain. Normal cats can be trained to stand freely on a platform tilted in the sagittal plane (pitch rotations) by variable angles (between -30° and +30°) from the horizontal (42). Trunk orientation is not stabilized in space but changes almost in parallel with platform tilt. This is due to the fact that the length and vertical orientation of the limbs vary little with platform tilt. The changes of limb length, though limited, occur in the direction one would expect on the basis of neck and vestibulospinal reflexes (44). Thus, nose-down tilts of the platform result in forelimb extension and hindlimb flexion, and opposite changes occur with nose-up tilts (37, 42).

The role of visual stimuli in the control of posture is demonstrated by the effect of dynamic pitch or linear vection of the visual surround around a stationary animal. These stimuli induce an illusory change of the subjective vertical and a transient perturbation of the equilibrium in both humans (7) and cats (49). Muscle responses are evoked at a long latency (about 100 ms), and limbs rotate in the same direction as the visual stimulus. Limb orientation returns to prestimulus values more than a second later (49). The vertical is normally estimated using multisensory information such as labyrinthine gravitoinertial and visual cues (54, 80). Because the head is effectively stabilized in space during posture and locomotion, it provides an inertial platform for monitoring both gravity direction and visual reference lines (63). The vestibulocollic and cervicocollic reflexes contribute to head stabilization in all directions, including pitch (5). The type of reflex interaction depends on the experimental conditions. These reflexes add and minimize changes in head position when the head is moved on a fixed body. By contrast, the reflexes oppose each other when the whole animal is moved: the vestibulocollic reflex tends to keep the head fixed in space, but the resulting head movement evokes a cervicollic reflex that tends to keep the head fixed to the body. The vectors of maximal activation of neck muscles in response to multidirectional rotations can be predicted by assuming that the coordinate transformation from semicircular canals to neck muscle coordinates minimizes the amount of muscle coactivation (61).

Also somesthetic stimuli influence body posture. First, they can affect the perception of body orientation in space (80). Thus aymmetric tactile stimuli spread over large contact areas of the body determine errors in psychophysical matching of the perceived vertical in humans (14) and can evoke righting reflexes in labyrinthectomized animals (75). It has been hypothesized that the subjective estimate of the vertical results from the combination of the gravity vector and an idiotropic vector aligned with the long axis of the body (27, 54). Somesthetic cues contribute to the latter. It is known that skin stimuli applied to the neck can induce changes in postural tone, with tonic flexion of the neck and forelimbs in cats (16). Abnormal somesthetic stimuli applied to the trunk of cats determine a profound disturbance of body posture (39). When cats wear a vest that is fitted to the shaved trunk, they tend to keep the limbs extended at a roughly constant orientation relative to a platform tilted in the sagittal plane, rather than relative to the vertical. This behaviour results in a progressive shift of the projected centre of mass up to the loss of balance at pronounced platform tilts. Cats seem to be induced to disregard information about highly abnormal weight distribution because of an alteration of the body scheme. The importance of somesthetic cues from the body in building an idiotropic estimate of the vertical is also underscored by observations on the posture adopted by blindfolded astronauts during exposure to microgravity (15). Somesthetic cues from the feet normally contribute to the perception of body orientation in space, as estimated from the perceived orientation of the ground reaction forces sensed by skin receptors and proprioceptors (17). Flexion-extension of the forepaw can modulate the gain of vestibulospinal reflexes (16a).

Lastly, stretch reflexes from the lower limbs can also contribute to stabilizing body posture. Their role is context-dependent (58). When calf muscles are stretched as a result of body sway determined by horizontal translation of the support platform, they are reflexly activated. When the same muscles are stretched as a result of a platform rotation under the feet, they exhibit small or no response. In fact, reflex activation compensates for body sway in the former condition, but would destabilize body posture in the latter condition (58). Thus the reflex gain is adapted according to the task.

II. *The problem of the controlled variables in posture.*

We have reviewed briefly the role of several feedback loops in postural mechanisms. Responses in limb and body muscles evoked by postural perturbations involve concurrent inputs from multiple sensory sources: visual, vestibular, and somatosensory. Each of these loops has its own set of input and output variables to monitor and control. However the coordinated action of the whole postural system is not effected muscle by muscle, but is presumably aimed at the control of more global goals (48, 51, 59). The nature of the controlled variable (or variables) has been the object of much investigation and debate (see 51).

The hypothesis of the stabilization of trunk orientation in space has been discussed in the previous section. As far as cat posture is concerned, the hypothesis is unsupported by the results with pitch rotations (42), and has not been tested quantitatively for roll and yaw. Trunk orientation might be better stabilized in humans, but only under special conditions (23, 51). For instance, when human subjects raise one leg sideways while standing, they must shift body weight on the supporting leg before the movement. Only trained subjects (dancers) succeed in stabilizing body posture without losing the alignment of the trunk axis with the vertical (57). Untrained subjects rotate the trunk away from the vertical and counterrotate the head.

According to a classical viewpoint, postural control can be equated with the stabilization of the body againts gravity, that is, with a problem of statics. Because animals are statically balanced when the vertical projection of their centre of mass (*pcm*) falls within the support area, it is often assumed that *pcm* is the global variable regulated in stance (13, 26, 51). Indeed *pcm* is maintained approximately constant under a variety of perturbed conditions, especially in bipedal stance where the support base is relatively narrow compared to body size (51).

An alternative hypothesis is that the maintenance of postural geometry takes precedence in the control hierarchy, *pcm* being determined only in a subordinate manner (37). Two global geometrical variables represent high-order parameters in the control of cat posture: the length and the angle of orientation relative to the vertical of each limb axis.[1] These variables are accurately controlled when the support platform is tilted in the sagittal plane (42), and when external loads tending to shift the body centre of mass are applied (37). Cats standing at the preferred interfeet distance align the axis of both fore- and hindlimbs with the vertical at widely different platform tilts, and keep the forelimbs relatively extended and the hindlimbs more flexed. Nose-down tilts of the platform result in a limited amount of hindlimb flexion (<5% of mean length per 10°-tilt), and forward rotation of the forelimbs (<2° per 10°-tilt). Opposite changes occur with nose-up tilts. (Changes

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[1] Limb movements associated with pitch of the support platform are essentially confined within a sagital plane. Accordingly, only the angle of vertical rotation (elevation) of the limb axis in the sagittal plane has been considered. The angle of horizontal rotation (yaw) should also be considered in the general case of the three dimensional movements, as when the platform is translated horizontally under the animal.

of forelimb length and hindlimb orientation are smaller and less consistent across animals.) Exactly the same behaviour is observed after the application of the load (corresponding to 20% of the animal's weight). Limb geometry is preserved unmodified after load application at the expense of marked changes in *pcm* (corresponding to an abnormal distribution of weight) and effort between forelimbs and hindlimbs (37). Thus the sum of the absolute values of joint torques at the forelimbs increases by about 60% over the control value.

Desired postural geometry is presumably defined on the basis of an internal model of the spatial relations of the body segments relative to each other and to the external environment according to the body scheme (23). The problem of the maintenance of balance can then be solved by complying with this body scheme that predicts limited changes of *pcm* under normal conditions (42). Even when this prediction fails under altered conditions, the animal may still attempt to adhere to the body scheme, as indicated by the absence of adaptation of postural geometry over 24 hours of continuous application of the external load (37). The CNS controls postural geometry directly rather than balance presumably because it has learnt that the preferred posture is stable under normal operating conditions. On the other hand, not only has posture largely evolved to oppose gravity for the maintenance of balance, but it is also organized in a reference frame that is anchored to the direction of gravity. As noted above, limb orientation is controlled relative to the vertical.

Balance constraints are more stringent for bipedal stance than for quadrupedal stance. In humans the position of the pelvis is stabilized in response to postural perturbations (26, 51). Because the centre of mass of human body is located close to the ilium, this strategy of positional control amounts to a control of *pcm*. Interestingly, similar kinematic strategies of *pcm* stabilization apply to postural responses evoked by external perturbations and to the anticipatory responses associated with the voluntary movements of the trunk involved in axial bending (51). Moreover, these kinematic strategies remain unchanged under microgravity, that is in the absence of equilibrium constraints (52). In sum, postural geometry is accurately controlled also in humans (23, 59) and the general principles of control do not differ substantially from those found in quadrupeds.

III. *Coordinate transformations for the control of posture.*

Length and orientation specify the position of the limb endpoint (the foot) relative to the proximal joint (scapula or hip) in a global manner, leaving the detailed geometric configuration undetermined. Desired endpoint position could be translated directly into appropriate patterns of muscle activities, as implied by some versions of the equilibrium-point hypothesis (25). However recent data provide evidence in favour of an intermediate processing stage that transforms endpoint coordinates (limb length and orientation) into the angular coordinates of the joints (39, 40, 48). To increase postural variability and replicate part of the normal behavioral repertoire, cats were trained to stand on the tilted platform (±20° from the horizontal), at variable interfeet distances (from -20% up to 40% of the mean preferred value), and head orientations (±60° in pitch and yaw). Postural responses to pitch involve changes in the elevation angles of three joints at either the forelimbs (scapula, shoulder and elbow) or the hindlimbs (hip, knee and ankle). The values of each angular coordinate varied substantially (by ~30° about the mean), as a result of the range of different experimental conditions. However these angles did not vary independently of each other, but covaried strictly. This was shown by representing the static geometric configuration of each limb in any given trial as one point in the three-dimensional (3D) space defined by the corresponding joint angles. The data points for all trials were not scattered throughout the 3D-space anatomically permissible, but were confined within a small volume close to one plane (39). The constraint of planar covariation does not depend on biomechanical factors, but is due to a neural control of limb geometry. In fact the orientation of the plane in the 3D-joint space is essentially the same in all cats (despite wide differences in their biomechanical parameters), and is also the same at the forelimbs and at the hindlimbs. The latter invariance is especially remarkable, considering that the forelimbs differ considerably from the hindlimbs in terms of the length and orientation of the individual corresponding segments. The described planar covariation involves absolute angles of orientation relative to the vertical at the proximal limb segments and relative angles of flexion-extension at the other joints. A planar covariation is also observed among all absolute angles, but with a worse residual variance. Irrespective of which one among these alternative sets of angles is the most appropriate to describe the constraint, it is clear that the process of coordinate transformation from endpoint coordinates to joint angles requires a reference to gravity. Interestingly, the application of anomalous somesthetic cues to the trunk perturbs not only the orientation of the limb axis relative to the vertical, but also the orientation of the plane of angular covariation in joint space (39). Coordinate transformations for postural control involve two distinct rules for the two global variables describing endpoint position: limb length maps in discrete, linear strips of 3D-joint space, whereas limb orientation maps in broad regions of joint space, allowing for one-to-many transformation of coordinates (see below).

The findings on static posture have been generalized to the dynamic responses evoked by unpredictable ramp rotations of the support platform in nose-down or nose-up direction (40). These responses describe complex paths that may diverge in different directions in the 3D-joint space; all paths, however, are confined close to the plane of static angular covariations. A notable finding has been that dynamic perturbations may evoke postural responses that involve a given path in one trial, but a completely different path in another trial, even though endpoint position remains essentially the same in both cases.

The results indicate that the coordinate transformation involves motor-equivalent solutions, that is, one-to-many mappings of endpoint coordinates into angular coordinates (40). Indeed the constraint of planar covariation imposes well defined boundaries to the admissible covariations of joint angles, but it allows at the same time a high degree of flexibility of specific geometrical configurations. The execution of a commanded change in the overall orientation of the limb is little sensitive to the joint configuration that is specifically chosen; it can be produced by means of a wide range of different changes in joint angles. This behaviour is characteristic of dynamical systems governed by chaotic attractors. Similar initial states (defined by the set of joint angles of a given limb) may evolve toward different final states. Arbitrarily small deviations (due to ubiquitous biological noise) from the initial state may lead to arbitrarily large deviations of the final state after sufficient time has elapsed. The essence of motor-equivalent behaviour is the continuous exploration of a wide region of joint angle space that is compatible with stability, and the reinforcement of the neural constraint. This is relevant not only from a motor-control viewpoint, but also from a sensory perspective. The multiplicity of different geometrical configurations of the limb that are enforced by the coordinate transformation tends to generate a correspondingly wide range of different configurations in sensory space. This allows the continuous recalibration of sensorimotor associations.

IV. *Independent control of limb position and ground reaction forces.*

A scheme of modular, distributed control of limb kinematics (position and movement) and kinetics (forces and torques) has recently been proposed (32, 38, 39). The scheme includes distinct, parallel paths. One path is hierarchically organized under the primacy of the control of limb geometry. Desired length and orientation of limb axis are initially prescribed and are subsequently transformed in the values of joint angles by means of the law of planar covariation. There exist two separate channels for the specification of length and for the specification of orientation. This is shown by the following observations: 1) the different dynamics exhibited by the changes in length and orientation in response to sinusoidal pitch (49) and ramp pitch (40); 2) pitch of visual surround about the stationary animal affects the orientation but not the length of the limbs (49); 3) length and orientation transform in joint angles following different rules (see above).

A different path in postural control involves limb kinetics. Ground reaction forces can be decomposed in normal and tangential components. Normal forces reflect directly the weight distribution among the limbs. In a previous section, we showed that weight distribution is subordinate to the control of limb geometry. Thus, desired limb geometry determines uniquely also the values of the normal forces. Tangential forces, instead, are controlled independently of limb geometry (38). Tangential forces have one of only two possible orientations (±45° from the anterior direction) during quiet stance (45). In response to platform translations in different horizontal directions, the forces actively generated tend to align with the same two orientations, whereas the passive forces are aligned with the direction of the perturbation (45). These results apply to long interfeet distances (*id*). The tangential forces rotate progressively in the lateral direction as the *id* is shortened (46). Studies of postural responses to pitch have indicated that the lever component of tangential forces is accurately partitioned between forelimbs and hindlimbs (39). However the specific proportions of this partitioning are highly variable among cats, in contrast with the stereotyped law of control of limb geometry (39). The law of control of lever tangential forces does not result in a distribution of the joint torques that is either optimal (minimizing the sum of absolute torques at all limb joints) or constant among cats. Thus although each cat adheres to a standard internal image of postural geometry, it has nonetheless its own idiosyncratic internal image of body stability and of the effort required.

V. *From posture to movement.*

The stabilization of posture is tightly integrated with the generation of movement. Anticipatory postural adjustments must generally take place before movement inception to compensate in feedforward manner the tendency to destabilize body posture arising from movement (51). Moreover, many movements involve not just a movement of an individual limb, but coordinated synergies of head, upper limbs, trunk and lower limbs. It is not surprising, therefore, that the concepts reviewed above for the control of posture are applicable to the control of movement as well (31, 32, 41). Diverse domains of motor behaviour are organized on the basis of similar general principles. Coordinate transformations from global variables describing target or endpoint location into the intrinsic coordinates of limb segment angles have been described for different tasks and animal species: arm reaching (43, 69) and drawing (70) in man, wiping reflex in the frog (6), avoidance reflex in the crayfish (30), and posture in cats (39, 40).

An application of these principles has recently been found also in the case of human locomotion (10). Locomotion consists of cyclic events controlled by central pattern generating networks (CPGs) that are located to a large extent within the spinal cord but are under the continuous influence of peripheral and descending signals (cf. 22). CPGs output complex patterns of muscle activity and regulate phase relations among different muscle groups. A common observation is that the time course of the changes in muscle activity and length, joint angles and torques can be variable not only across speeds and subjects, but even from trial to trial (60, 79). However, it has been found that the changes in the elevation of lower limb segments with respect to the vertical show stereotyped patterns in all subjects (10). Waveforms of the elevation angles at pelvis, thigh, leg and foot do not change shape, but only scale in time and magnitude as a function of the speed of locomotion. Dissociation of the behaviour of the orientation angles from that of the joint angles is possible in a redundant limb, that is a limb whose degrees of freedom of angular motion exceed in number the degrees of freedom of endpoint motion. Multiple geometrical configurations are then compatible with the same endpoint position. A similar dissociation has been also observed in the case of reaching and drawing movements of the arm (43, 70).

The changes of the elevation angles at each limb segment are tightly coupled by a strong constraint (10). Despite the large excursion of the individual angles, the global geometric configuration of the limb lies very close to one plane in the four-dimensional space of the elevation angles (pelvis, thigh, leg, foot). The temporal changes of these angles describe a cyclic loop during each gait cycle whose residual variance around the best-fitting plane is less than 1% of the total experimental variance. This law of intersegmental coordination is reminiscent of that previously described for the control of cat posture (39, 40). Intersegmental coordinations are defined with respect to the vertical direction in the case of both postural responses and locomotion. That similar laws of intersegmental coordination apply to the control of posture and locomotion is functionally significant, in as much as locomotion must assure a forward progression compatible with dynamic equilibrium, adapting to potentially destabilizing factors (e.g. uneven terrain, obstacles etc.) in an anticipatory fashion by means of co-ordinated synergies of the whole body (18, 24).

It is important to stress that intermediate representations in angular coordinates are not a logical necessity, given *a priori*. Different computational schemes predict direct transformations of commanded changes of endpoint coordinates in the appropriate values of joint torques (76) or muscle forces (8). A possible *raison d'être* of representations in the intrinsic space of joint angles is that the kinesthetic information about limb geometry is coded in such a coordinate system (71). Thus the coordinate transformation would allow a comparison between the desired change of endpoint position (coded in the efferent copy of motor commands) and the resulting motion of the limb as sensed by peripheral feedbacks.

The neural algorithm used to implement the coordinate transformations is not the same in all cases. For arm reaching and drawing, target location is defined in shoulder-centred spherical coordinates (distance, elevation and azimuth) and linearly mapped in yaw and elevation angles of the upper arm and forearm (69, 70). For locomotion, foot position in front of the subject is defined in hip-centred spherical coordinates and mapped nonlinearly in the elevation angles of the lower limb (10). This implies that limb trajectories are highly stereotyped in terms of both endpoint (hand or foot) motion and angular motion (31). In the case of the wiping reflex of the frog (6) and cat posture (40), the opposite behaviour is found. The coordinate transformation involves motor-equivalent solutions: any given endpoint position can be achieved using many different combinations of joint angles.

Another principle of organization of postural systems that applies also to movement is given by the existence of parallel, distributed modules for the control of kinetics and kinematics (38). Grasping and manipulation of objects are especially developed in primates. These tasks require accurate control not only of hand position to reach the object, but also of the contact forces at the fingers-object interface (28), just as the maintenance of posture requires a control of limb position and ground contact forces. The control of contact forces, in turn, can be accomplished by means of a modulation of the overall stiffness and viscosity of the limb. It has recently been shown that limb stiffness and viscosity are centrally modified in anticipation of a pre-planned dynamic interaction with an object of known properties, such as that involved in catching a free-falling ball, whose mass and height of fall can be changed experimentally (34). Moreover, stiffness and viscosity can be tuned independently of each other, and independently of limb geometry (35). Tuning of these mechanical parameters is accomplished by means of anticipatory muscle co-activation and a centrally gated reversal of short-latency stretch reflexes in elbow and wrist muscles (33).

VI. *Gravity-referenced spatial representations in central neural structures.*

We do not review the localization and role of the distributed networks involved in postural control (e.g. 51), but focus only on possible neural substrates for encoding limb and body position in gravity-based reference frames. A vector code of movement direction has been described at the level of motor and premotor cortex, basal ganglia and cerebellum (20). Neurons are broadly tuned to the direction of hand movement. Activity is maximal along a preferred direction and decreases proportionally to the cosine of the angle between this direction and the direction of actual movement. Preferred directions are distributed uniformly throughout space. The direction of actual hand movement is prescribed by the overall activity of the ensemble population. Each neuron contributes a vector in its preferred direction with an amplitude proportional to the level of activity during actual movement direction. Population vectors predict movement trajectory during reaching (20). Accurate limb positioning under visual guidance is controlled by the same pathway from motor cortex to the cervical propriospinal system both in reaching and in locomotion (1, 21). A neural substrate for a gravity-based and body-centred positional code has recently been found in the superior parietal lobule of the monkey (36). Neural activity is monotonically tuned in a frame of reference whose coordinates define the azimuth, elevation and distance of the hand relative to the shoulder. Each spatial coordinate is encoded in a different subpopulations of neurons. This parcellation is perhaps a neural correlate of the observation derived from behavioral studies that these spatial parameters are processed in parallel and largely independent of each other.

Vestibulospinal and reticulospinal tracts encode postural responses of the limbs in a gravity-based, head-centred frame (9, 12, 61c, 77). In locomotion afferent information from the moving leg and efferent copy from spinal locomotor networks are sent to cortical and subcortical centres via the ventral and dorsal spinocerebellar tracts (4). DSCT neurons are broadly tuned to the length and vertical elevation of the hindlimbs (11), that is the same coordinates described in behavioral studies on cat posture (42). Encoding posture and movement at different neural sites in similar, gravity-based frames would allow alignment in register of spatial information derived from multiple sensors and directed to multiple effectors.

SUMMARY

Studies are reviewed that address the problem of the variables controlled in the maintenance of body posture and generation of limb movement. Vestibulospinal and neck reflexes cancel each other in response to roll, but not in response to pitch of the animal. In pitch trunk orientation is not effectively stabilized in space. Instead, limb length and orientation relative to the vertical are accurately controlled in normal cats pitched statically and dynamically by variable angles. Control of limb geometry may even take precedence over the control of the projected centre of mass. Coordinate transformation results in a constraint of planar covariation of the elevation angles at all limb segments in cat posture. Because the same constraint applies also to human locomotion, we suggest that sharing the same laws of intersegmental coordination for the control of posture and locomotion helps to assure the maintenance of dynamic equilibrium during movement. Moreover, because several neural sites encode posture and movement in gravity-based reference frames, alignment in register of spatial information derived from multiple sensors and directed to multiple effectors is made possible.

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